NeuroImage 147 (2017) 692–702

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Beta-band activity represents the recent past during episodic encoding

Neal W Morton[a,*], Sean M. Polyn[b]

[a] The University of Texas at Austin, Center for Learning & Memory, 1 University Station Stop C7000, Austin, TX 78712-0805, United States
[b] Vanderbilt University, Department of Psychology, PMB 407817, 2301 Vanderbilt Place, Nashville, TN 37240-7817, United States

ARTICLE INFO

Keywords:
Episodic memory
Memory search
Clustering
Computational model

ABSTRACT

While much research has focused on understanding how individual stimuli are encoded in episodic memory, less is known about how a series of events is bound into a coherent episode. Cognitive models of episodic memory propose that information about presented stimuli is integrated into a composite representation reflecting one's past experience, allowing events separated in time to become associated. Recent evidence suggests that neural oscillatory activity may be critically involved in this process. To examine how oscillatory activity contributes to binding of information across events, we measured scalp EEG as participants studied categorized lists of people, places, and objects. We assessed their memory for the lists using free recall, allowing us to characterize the temporal and semantic organization of the studied items in memory. Using pattern classification, we identified EEG activity during encoding at a range of frequencies and scalp locations that was sensitive to the category of presented stimuli. In the beta band (16–25 Hz) at right posterior electrodes, we observed activity that was also sensitive to the category of recently presented stimuli. This neural activity showed two characteristics consistent with a representation of the recent past: It became stronger when multiple items from the same category were presented in succession, and it contained a fading trace of the previous category after a category shift. When items were separated by an inter-item distraction task, this integrative beta-band activity was disrupted. Distraction also led to decreased semantic organization of the studied materials without affecting their temporal organization; this suggests that distraction disrupts the integration of semantic information over time, preventing encoding of items in terms of the semantic context of earlier items. Our results provide evidence that beta-band activity is involved in maintaining information about recent events, allowing construction of a coherent representation of a temporally extended episode in memory.

Introduction

Everyday life can be thought of as an ever-unfolding series of events containing specific people, places, and things (Zacks and Tversky, 2001). The details of these events are interpreted and given meaning by the semantic memory system (Rogers and McClelland, 2004) and linked to a specific spatial and temporal context by the episodic memory system (Tulving, 1983; Schacter, 1987). When an experimental participant views a picture of a person, a place, or a thing, fMRI and scalp EEG recordings reveal multivariate neural activity patterns that are sensitive to the category of the stimulus (Haxby et al., 2001; Kriegeskorte et al., 2008; Newman and Norman, 2010; Fuentemilla et al., 2010). The fidelity of category-specific patterns of brain activity can be estimated using pattern classification (Norman et al., 2006) and has been related to performance in a number of memory tasks. When studying an item for a later memory test, the fidelity of category-specific activity is predictive of subsequent memory for that item (Kuhl et al., 2012; Morton et al., 2013). Distributed category-specific activity has also been linked to working-memory maintenance (Fuentemilla et al., 2010; LaRocque et al., 2013) and retrieval from long-term memory (Polyn et al., 2005; Morton et al., 2013). While studies using multivariate methods to track category-specific activity patterns have provided valuable information about how individual items are encoded in memory, questions remain about how representations of individual items are woven together into a coherent episode.

Work using the free-recall paradigm has provided insight into how people encode and retrieve memories of a series of events. In free recall, an episode unfolds as a series of study events and is followed by a memory search period in which the participant is given a general prompt to recall all of the studied material in whatever order it comes to mind. Organizational analysis of the sequence of recall responses reveals reliable effects of the temporal and semantic structure of the study experience. Temporal organization exhibits itself as a tendency to successively recall items that were neighbors in the study list, and

* Corresponding author.
E-mail address: neal.morton@austin.utexas.edu (N.W. Morton).

http://dx.doi.org/10.1016/j.neuroimage.2016.12.049
Received 10 August 2016; Accepted 18 December 2016
Available online 21 December 2016

semantic organization is observed as a tendency for participants to successively recall items with similar or related meanings (Bousfield, 1953; Puff, 1979; Howard and Kahana, 2002b; Kahana, 2012). These organizational phenomena have been used to guide the development of computational models of episodic memory, including buffer models (Raaijmakers and Shiffrin, 1980; Sirotin et al., 2005; Kimball et al., 2007; Davelaar et al., 2005) and retrieved-context models (Howard and Kahana, 2002a; Sederberg et al., 2008; Polyn et al., 2009; Lohnas et al., 2015).

While there are structural differences between buffer models and retrieved-context models, both classes of models propose that there is a cognitive representation that integrates information about presented stimuli over time, allowing items that are presented at different times to become associated. This mechanism allows both classes of models to account for the finding of temporal organization (Kahana, 1996; Howard and Kahana, 2002a). In buffer models, item representations are maintained in a form of short-term storage, facilitating the formation of inter-item associations. Neighboring items in the list tend to be in the buffer at the same time; as a result, they are more likely to become associated, leading to temporal organization during free recall. In retrieved-context models, information about each presented stimulus is integrated into a gradually changing representation of the temporal context of the study episode. During free recall, retrieving an item triggers reactivation of its associated context, which provides a strong cue for items that were presented near to the retrieved item in the list.

In both classes of models, during study the memory system constructs a composite representation reflecting the recent history of presented stimuli, and the operation of this representation is critical for determining the order in which items are retrieved during later memory search. A neural correlate of such a representation should meet two criteria: (1) it should be sensitive to the content of presented stimuli (e.g. having different patterns for different stimulus categories) and (2) it should reflect the recent history of presented stimuli in addition to currently presented stimuli. Because this type of neural activity integrates information about presented stimuli over time, we refer to a signal with these properties as an *integrative* signal. Because this type of integrative representation contains information about presented stimuli, it contrasts with other types of models that assume that stimuli become bound in a mental timeline that is either based purely on elapsed time (Brown et al., 2007) or on a randomly changing representation that evolves independently of studied stimuli (Estes, 1955; Mensink and Raaijmakers, 1989).

Over the past several years, a number of studies have found evidence for integrative neural signals related to episodic retrieval (Jenkins and Ranganath, 2010; Manning et al., 2011; Morton et al., 2013; DuBrow and Davachi, 2014; Hsieh et al., 2014). Morton et al. (2013) examined category-specific oscillatory activity recorded with scalp EEG, and observed category-specific patterns that contained information not just about the currently viewed stimulus, but also about the recent history of presented stimuli. This is consistent with a number of studies suggesting that oscillatory activity is critically involved in the maintenance of information about recently presented stimuli (Lisman and Idiart, 1995; Howard et al., 2003; Axmacher et al., 2010; Fuentemilla et al., 2010). In the Morton et al. (2013) study, patterns of oscillatory activity related to stimulus category increased in fidelity as multiple items from the same category were presented in succession. Furthermore, the rate of this increase was related to the dynamics of memory search: A sharper increase in category specificity of neural activity during the study period predicted increased semantic organization during the recall period. Consistent with buffer and retrieved-context models, these results suggest that oscillatory neural activity during episodic encoding integrates information about stimuli over time, facilitating later retrieval.

However, a number of important questions remain. First, to improve accuracy when decoding stimulus category, Morton et al. (2013) pooled information over a range of frequencies and electrodes, obscuring the specific characteristics of the neural activity that gave rise to these effects and leaving open the question of what frequency bands and electrodes are involved. Second, in order to demonstrate integration, they showed that category-specific activity increased in strength as a person studied a series of items from the same category. They did not test another important prediction related to integration, predicted by both buffer and retrieved-context models: after the study sequence shifts from one category to another, neural activity related to the previously presented category should fade gradually. Such a finding would be diagnostic of an integrative account and would provide evidence against alternative interpretations of their findings.

Attentional models provide a potential alternative explanation to the integrative account outlined above. For example, as a series of items from a particular category is studied, the attentional system could emphasize prototypical category features of the items. This would result in an emphasizing of category-specific features during a series of items from the same category, and could account for a progressive increase in category-specific activity. However, because this account is based on altered processing of stimuli that are being viewed currently, this alternative would not predict the gradual fade of neural signals related to a prior category.

Finally, both buffer models and retrieved-context models make a clear prediction for how distraction during encoding should affect cue construction. Both classes of models propose that performing a distraction task disrupts the integration process, either by forcing item representations out of the short-term buffer (Raaijmakers and Shiffrin, 1981; Davelaar et al., 2005), or by integrating distraction-task information into temporal context (Sederberg et al., 2008). Therefore, if integrative category-specific oscillatory activity reflects such a process, it should be disrupted by distraction, and this disruption should affect how memories are encoded.

In order to better understand the neural mechanisms underlying integration during episodic encoding, we measured scalp EEG as participants studied lists of categorized stimuli for free recall, and used pattern classification techniques to decode information related to stimulus category. We varied the amount of distraction between studied items, with the prediction that distraction would disrupt the accumulation of category-specific neural activity during encoding. In order to maximize the reliability of category decoding estimates, which rely on training a classifier to decode participant-specific patterns of oscillatory activity, we collected EEG data during 1296 study events for each participant across three recording sessions. This allowed us to characterize the specific topography and frequency range of integrative oscillatory activity and examine its involvement in episodic memory formation.

Materials and methods

Participants

Ten paid volunteers (5 female, age 18–30 years) participated in the study. In order to ensure full effort, participants received a performance-based bonus of up to $10 for each session. The research protocol was approved by the Institutional Review Board of Vanderbilt University.

Materials

Each study item was a photograph of a famous landmark, a contemporary celebrity face, or a common object, paired with a sound clip of the item's name. There were 256 items in each category. The pool was based on a previous experiment (Morton et al., 2013), with some changes to increase the homogeneity of the items within each category. Pictures were taken from publicly available sources. All pictures were cropped and scaled to 600×750 resolution. For each celebrity, a picture was selected to maximize image quality, emotionally neutral expression, facing straight toward the camera, and simplicity of the background. Pictures were cropped approximately from the chin to the top of the head (excluding hair). Items were chosen to limit overlap with the other categories (e.g. the Liberty Bell was not included, since it could be considered either a location or an object). With the exception of two performance venues (known most for their interiors), all locations were shown from the exterior and taken during the day. Finally, all object pictures were taken on a white background. Using the SHINE toolbox (Willenbockel et al., 2010), images were converted to grayscale and normalized so that mean image intensity and contrast were the same for each image.

Names of studied items were presented auditorially in order to limit eye movements during encoding (in contrast to the study reported by Morton et al., 2013, which used visual presentation). A male speaker (NWM) recorded sound clips of all item names with neutral affect. Sound clips ranged in duration from 690 to 1498 ms (overall: mean 1056, S.D. 159; celebrities: mean 1105 ms, S.D. 104 ms; locations: mean 1166 ms, S.D. 124 ms; objects: mean 898 ms, S.D. 104 ms).

Experimental paradigm

In a preliminary session, participants rated their familiarity with each item while scalp EEG was recorded. This allowed us to assess participants' pre-experimental familiarity with each item and provided participants at least a minimal familiarity with each item. Items were presented in blocks, each of which contained 24 items, with 8 items from each category. The order of item presentation within each block was designed to match the structure of item presentation in the later free-recall sessions (described below). Each item was presented for 2000 ms, during which participants rated their familiarity with the item on a four-point scale. The name of the item was presented auditorially, beginning at the same time the image was presented. Participants were given a chance to rest after each block. The familiarization session included 32 blocks; all 768 items were presented.

The subsequent 3 sessions each included 18 free-recall trials, followed by a final free recall period; scalp EEG was recorded throughout each session. In each free-recall trial, 24 items were presented, with 8 items from each of the 3 categories. Within each study list, items from the same category were presented in succession, in trains of 3–5 items. The order of the trains was randomized, with the constraint that all categories appeared in each consecutive set of 3 trains, and that adjacent trains did not contain the same category. Highly similar items (e.g., stadiums, presidents, musical instruments, celebrities with the same first name) did not appear in the same list.

There were three types of lists: immediate free recall (IFR), short continual distraction free recall (CDS; 2.5 s of distraction), and long continual distraction free recall (CDL; 7.5 s of distraction). In the IFR condition, each item (including a picture and corresponding sound clip) was presented for 2000 ms; during this interval participants rated how much they liked or disliked the item on a 4-point scale. Each item presentation was followed by a fixation cross for 1000 ± 200 ms. After the last item in the list, a fixation cross was presented for 1300 ± 100 ms, followed by a row of asterisks and a 300-ms tone signaling the start of a 70-s free-recall period. Participants were instructed to say the names of items from the list in any order, and to keep trying to remember items throughout the recall period. Digital recordings of vocal recalls were scored using Penn TotalRecall (available at: http://memory.psych.upenn.edu/TotalRecall).

The CD conditions were the same as the IFR condition, except each item was preceded and followed by a math distraction task. After each item, a fixation cross was presented for 500 ± 200 ms. Next, a series of three digits was presented, each for 400 ms (with no gap in between). After the digits, a proposed answer was immediately shown along with a question mark until the participant responded or the distraction period ended. Participants were instructed to indicate by button press whether the last number equaled the sum of the first three numbers. The proposed answer was incorrect for 50% of problems; incorrect answers were generated by adding 1, −1, 2, or −2 to the correct answer. Immediate feedback was given in the form of a beep to indicate incorrect responses. After the response, a fixation cross was presented for 300 ± 200 ms. Another problem was presented if there was at least 2400 ms left in the distraction period; otherwise, a fixation cross was presented for the remainder of the distraction period. Each distraction period was followed by a fixation cross for 500 ± 200 ms. Distraction period timing was designed so that participants were presented with one problem in the 2.5 s condition, and up to three problems in the 7.5 s condition.

In order to encourage participants to focus on the distraction task rather than rehearsing items from the list, participants were informed that half of the bonus payment for each session would be based on the total number of math problems solved in that session. One fourth of the bonus for each session was based on the average number of items recalled in each list, and another fourth was based on how consistently the participant made the like/dislike judgment within 2 s of stimulus onset.

Each of the three free-recall sessions included 18 lists, 6 from each condition. Conditions were randomly assigned to lists, with the constraints that each group of three lists included all conditions, and no adjacent lists were from the same condition. Each item appeared in a maximum of one list in each session, but could appear in multiple sessions. At the end of each session, there was a final free recall (FFR) period where participants were given 360 s to recall names of items from any of the lists presented during the session.

Behavioral analysis

In addition to standard measures of free-recall performance such as recall as a function of serial position, we also calculated measures of recall organization. We measured two forms of recall organization: temporal organization and category organization. Temporal organization refers to a tendency to successively recall items that were presented near to each other in the study list, while category organization is a tendency to successively recall items from the same category. To estimate temporal organization independently of category organization, we examined recall transitions between items from the same category. For these within-category transitions, we calculated the temporal organization score (Polyn et al., 2009). Each within-category recall transition is between two items, the *just-recalled* item and the *next-recalled* item. Given a particular just-recalled item, we calculated the set of possible next-recalled items (i.e. all items from the same category that had not already been recalled). These possible next-recalls were labeled with their distance (in terms of serial position in the list) from the just-recalled item. These distances were rank ordered, and the percentile rank of the actual next-recalled item was recorded. The average of these percentile scores was calculated over all within-category transitions to obtain a summary measure of temporal clustering, with higher values indicating greater clustering. A similar technique was used to characterize temporal organization for between-category transitions. Category organization was measured using the semantic list-based clustering measure (LBC_{sem}; Stricker et al., 2002).

Scalp electroencephalography recordings and data processing

EEG measurements were recorded using 128-channel HydroCel Geodesic Sensor Nets and a Net Amps 300 Amplifier (Electrical Geodesics, Inc.). Recordings were initially referenced to Cz. Voltage was digitized at 500 Hz , and a digital bandpass filter of $0.1 - 200$ Hz was applied.

A digital Butterworth notch filter with zero phase distortion at 60 Hz was used to remove electrical noise. Electrodes with poor contact were identified through manual inspection of event-related potential (ERP) images (Jung et al., 2001); these electrodes were omitted from the independent components analysis (ICA) procedure described below. Continuous EEG was segmented into epochs during the study period of free-recall trials, from 2000 ms before stimulus onset to 1500 ms after stimulus offset. Epochs were manually inspected using EEGLAB (Delorme and Makeig, 2004) to reject epochs containing non-stereotyped artifacts such as skin potentials. ICA was then used to decompose the signal (Onton et al., 2006). Components reflecting artifacts, such as eye movements, blinks, and muscle artifacts, were manually identified; non-artifactual components were projected back into the original sensor space to obtain a cleaned signal (Junghöfer et al., 2000; McMenamin et al., 2010). Bad electrodes were then replaced using spherical spline interpolation (Nolan et al., 2010).

Remaining artifacts on individual electrodes on specific epochs were removed using spherical spline interpolation. Our procedure was based on a combination of the SCADS (Junghöfer et al., 2000) and FASTER (Nolan et al., 2010) artifact-rejection methods. Bad electrode-epochs were detected using a number of statistics; this procedure is modified from the FASTER algorithm proposed by Nolan et al. (2010). For each epoch, an electrode was considered bad if there was a voltage range of greater than 150 μV, or if the electrode-epoch was an outlier (defined as more than six times the interquartile range above or below the first or third quartile, relative to all electrode-epochs) on any of three statistical measures. Because the variance of different electrodes depends on their distance from the reference, quadratic regression was used to estimate the effect of distance from reference on each of the statistics; rejection was performed on the residuals of this regression (Junghöfer et al., 2000). The first statistic is designed to detect fast changes related to muscle artifacts. First SS_{fast} is calculated as the sum of squared differences between successive samples; SS_{fast} is then divided by the total summed squared deviations, SS_{total}, to obtain a measure proportional to the fraction of variance in voltage explained by fast changes. Manual inspection confirmed that this measure has high sensitivity and selectivity for detecting EMG artifacts. The other statistics are the variance over time and the difference between the maximum and minimum voltages. Any electrodes identified as bad for a given epoch were replaced using spherical spline interpolation (Nolan et al., 2010). If more than 10% of electrodes were bad for a given epoch, that epoch was excluded. After interpolation of bad electrode-epochs, the data were converted to an average reference. Finally, the electrode-epoch interpolation procedure was run again on the re-referenced data (Junghöfer et al., 2000).

Oscillatory analysis

We measured oscillatory power using a Morlet wavelet transform with a wavenumber of 6. Oscillatory power was measured at 37 logarithmically spaced frequencies from 2 to 128 Hz. Power was then log-transformed and down-sampled to 25 Hz. Log power was normalized relative to a baseline period 500–400 ms before stimulus onset, based on the mean and standard deviation of power over epochs, calculated individually for each session.

Multivariate pattern analysis

We used multivariate pattern analysis (Norman et al., 2006) to decode stimulus category based on patterns of oscillatory power (Newman and Norman, 2010; Morton et al., 2013). Classification was carried out using penalized logistic regression (penalty parameter=10), using L_2 regularization (Duda et al., 2001). Classification analyses were carried out using Aperture (available at: http://mortonne.github.io/aperture/) and the Princeton MVPA Toolbox (available at: http://www.pni.princeton.edu/mvpa). A cross-validation procedure was used to determine the strength of category-specific activity during each item presentation, based on the distributed pattern of oscillatory power during the corresponding epoch. The classifier was trained on all but one list, then applied to the epochs on the left-out list to evaluate its performance, measured as the fraction of items classified correctly.

We first examined which frequencies, times relative to stimulus onset, and electrodes contained information about stimulus category. First, to characterize how category information varied by time and frequency, a separate classification analysis was performed at each time and frequency bin, to decode category based on the pattern of oscillatory power over the scalp. We next examined the category discriminability of oscillatory activity at each individual electrode. At each electrode, we carried out a classification analysis where the classifier simultaneously used features taken from two time bins (power was averaged within these bins: 0–500 ms and 500–2000 ms) and all frequencies. An average linkage clustering technique was then used to sort electrodes into high- and low-performance clusters. This technique identified clusters based on the average difference in classification performance between each pair of electrodes, and was used to define two regions of interest (ROIs) where classification accuracy was highest (see Results for details).

Fig. 1 provides a schematic overview of the approach used for subsequent analysis, which focused on six frequency bands of interest: delta (2–4 Hz), theta (4–8 Hz), alpha (10–14 Hz), beta (16–25 Hz), low gamma (25–55 Hz), and high gamma (65–128 Hz). Power was averaged within each of these ranges to obtain power values for each band. For each electrode and frequency band, we performed a cross-validation analysis, with power at each time bin during stimulus presentation (0–2000 ms, sampled at 25 Hz) as features. Classifier performance was then averaged over all electrodes within each ROI.

At each electrode and frequency band, we calculated the classifier evidence of the category of each item, based on its neural activity over time (shown for an example item presentation in Fig. 1B). We averaged this evidence over all electrodes in each ROI. For each ROI/frequency band, we calculated the average classifier evidence as a function of the position of the item in a train of items from the same category, separately for each subject (as shown schematically in Fig. 1C). For each subject, we calculated the slope of classifier evidence over the first three train positions. We focused on the first three train positions because Morton et al. (2013) found that classifier evidence did not increase beyond the third train position, and because in this study the first three train positions occurred more frequently than later positions (the minimum train length was three). For each subject, we used linear regression to determine the slope of mean classifier evidence as a function of train position. We used a t-test to assess whether the slope over train position was significantly positive across subjects. Significance values were Bonferroni corrected across ROIs, frequency bands, and distraction conditions. The classifier evidence values were also used to track activity related to the previous category and a baseline category, which was neither the current nor previously presented category (Fig. 1C).

Results

Inter-item distraction decreases recall performance

We examined recall performance in the different experimental conditions: immediate free recall (IFR; no distraction), continual distraction–short (CDS; 2.5 s of distraction before and after each item), and continual distraction–long (CDL; 7.5 s of distraction). Results from a pilot study suggested that the effect of distraction on recall varied between recency positions (i.e., later positions in the list associated with elevated recall) and non-recency positions (all earlier positions). Therefore, to characterize effects of distraction on recall performance, we first divided serial positions into recency and non-recency positions. To determine the boundary between these groups, we examined average performance across the three conditions. Starting with the first serial position, we conducted paired t-tests comparing

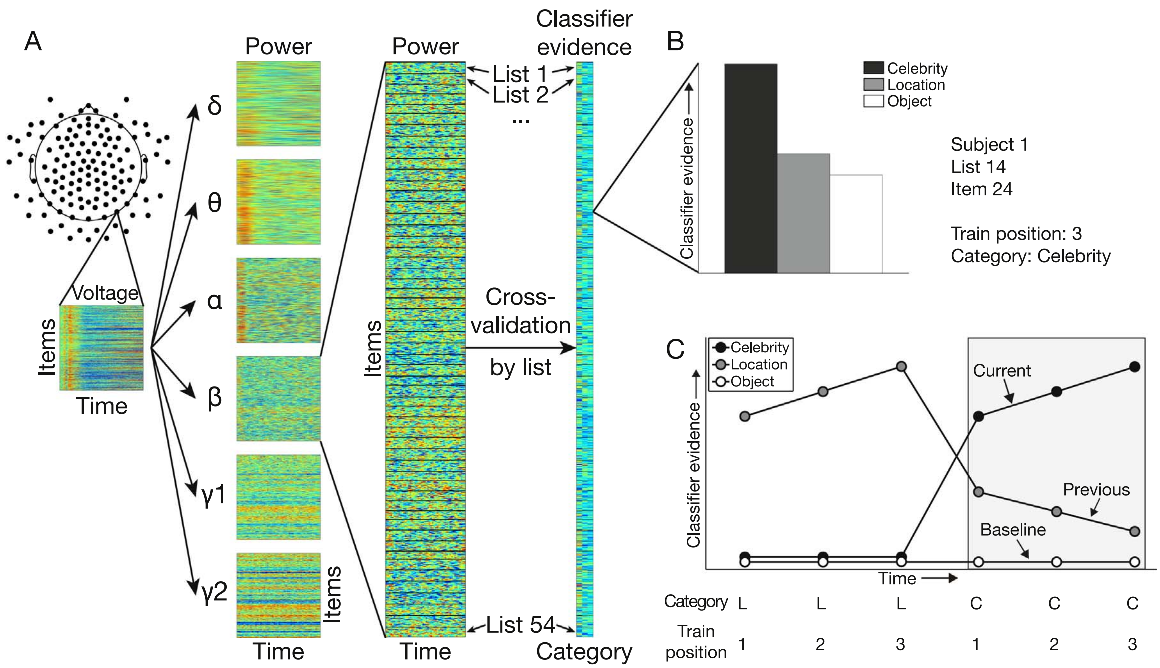

Fig. 1. Overview of the main classification analysis. (A) At each electrode of interest, voltage was sampled around the time of each item presentation. Oscillatory power (in six frequency bands and 50 time bins) was estimated for each item. Power estimates at each time bin were used as features in a pattern classification analysis to decode stimulus category. (B) For each electrode and frequency band, this classification analysis produced an estimate of the strength of each category representation (referred to as classifier evidence) during each item presentation. (C) A schematic of the predicted signature of persistent category-specific activity, for the first six items of an example list. Sets of same-category items are presented successively, with each item assigned a train position indicating its position within the set (here, a train of three locations is presented, followed by a train of three celebrities). For each item, classifier evidence for each category was labeled as belonging to the category of the current train, the category of the previous train, or a baseline category that had not been presented recently. If there is persistent category-specific activity, we predict that classifier evidence for the current category will increase with train position, while classifier evidence for the previous category will decrease with train position (as shown in the shaded box). $\gamma1$: low gamma; $\gamma2$: high gamma.

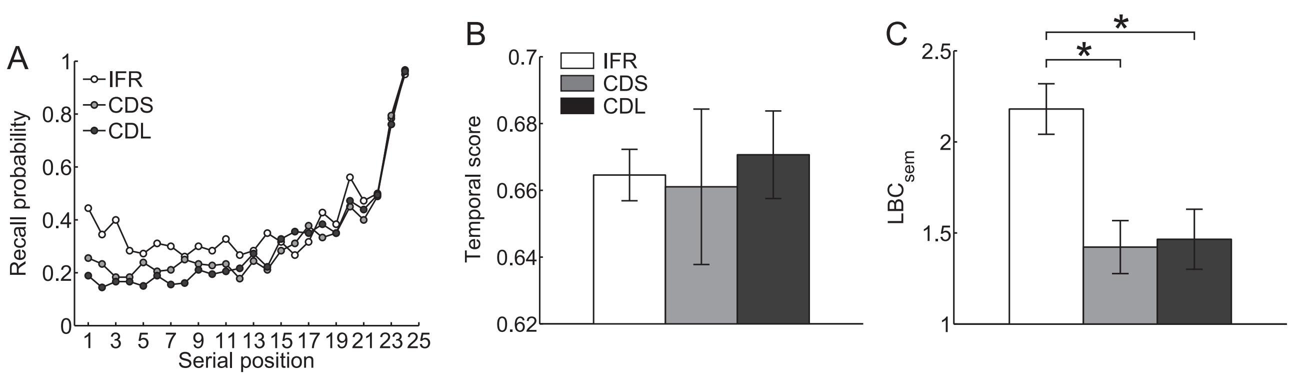

Fig. 2. (A) Recall probability by serial position, for each distraction condition. (B) Distraction had no effect on temporal organization scores. To control for the effect of category, only within-category transitions were included. (**C**) Distraction significantly attenuated category clustering, as measured by LBC$_{sem}$. IFR: immediate free recall; CDS: short continual distraction; CDL: long continual distraction. Error bars indicate standard error of the mean.

recall probability at each serial position to recall probability at the serial position after it. Serial positions 12 and 13 were the earliest pair to show a reliable increase in recall ($t(9) = 1.96$, $p = 0.041$, one-sided test). We therefore divided serial positions into two bins: early (i.e. non-recency; 1–12) and late (i.e. recency; 13–24), and carried out a two-way repeated measures ANOVA with Greenhouse-Geisser correction for nonsphericity to examine the influences of serial position and distraction on recall performance (Fig. 2A). The ANOVA revealed a significant main effect of serial position bin ($F(1, 9) = 296.9$, $p = 3.4x10^{-8}$), a main effect of distraction ($F(2, 18) = 31.74$, $p = 1.4x10^{-6}$), and an interaction ($F(2, 18) = 13.98$, $p = 0.00063$). Followup one-sided t-tests tested the prediction that recall would decrease with increasing distraction. For early positions, there was a significant decrease in recall performance between IFR and CDS ($t(9) = 8.20$, $p = 9.1x10^{-6}$), between IFR and CDL ($t(9) = 9.26$, $p = 3.4x10^{-6}$), and between CDS and CDL ($t(9) = 2.29$, $p = 0.024$). At late positions, there was a significant decrease between IFR and CDS ($t(9) = 2.18$, $p = 0.029$); all other pairwise comparisons were not significant ($p > 0.05$). The progressive decrease in recall performance from IFR to CDS, and from CDS to CDL, suggests that our parametric manipulation of distraction had a progressive effect on memory search processes. The relative insensitivity of late positions to distraction duration is consistent with prior work characterizing the insensitivity of the recency effect to changes in the temporal spacing of studied items (Glenberg et al., 1980; Howard and Kahana, 1999; Lohnas and Kahana, 2014).

Inter-item distraction dissociates temporal and semantic organization

We measured temporal clustering (the tendency for successive recall responses to come from neighboring list positions) using the temporal organization score introduced by Polyn et al. (2009). In order to control for the influence of semantic organization, we separately characterized temporal clustering for within-category and between-category recall transitions (Polyn et al., 2011). Significant temporal clustering (a temporal organization score >0.5) was observed for within-category recall transitions in all three experimental conditions (Fig. 2B; IFR: $t(9) = 21.37$, $p = 5.1x10^{-9}$; CDS: $t(9) = 6.92$, $p = 6.9x10^{-5}$; CDL: $t(9) = 13.02$, $p = 3.8x10^{-7}$). There were no significant differences in within-category temporal organization between conditions (all $p > 0.05$). Similar results were observed for between-category transitions. There was significant temporal organization in between-category transitions for all distraction conditions (IFR: mean 0.554, SEM 0.011, $t(9) = 49.47$, $p = 2.8x10^{-12}$; CDS: mean 0.595, SEM 0.020, $t(9) = 30.48$, $p = 2.2x10^{-10}$; CDL: mean 0.577, SEM 0.011, $t(9) = 52.14$, $p = 1.8x10^{-12}$). The distraction conditions did not differ in the amount of temporal organization observed in between-category transitions (all pairwise comparisons $p > 0.05$). Consistent with prior results (Howard and Kahana, 1999), although recall performance was decreased in the distraction conditions, distraction had no effect on the temporal organization of recall.

We also examined organization in terms of the semantic features of the list, in the form of category clustering (a tendency for successive responses to come from the same category). We quantified this phenomenon with the list-based semantic clustering (LBC_{sem}) measure introduced by Stricker et al. (2002). Category clustering was decreased in the distraction conditions relative to IFR (Fig. 2C). Category clustering in IFR was greater than in CDS ($t(9) = 4.18$, $p = 0.0024$) and CDL ($t(9) = 5.22$, $p = 5.5x10^{-4}$). There was no difference in clustering between CDS and CDL ($t(9) = 0.29$, $p = 0.78$).

In summary, strong temporal and category organization was observed in the absence of distraction. While temporal organization was not affected by either level of inter-item distraction (Howard and Kahana, 1999; Lohnas and Kahana, 2014), category organization was attenuated even in the short-distraction condition. We did not observe evidence that increasing the amount of inter-item distraction led to a further decrease in category organization.

Neural category discriminability during encoding

In order to characterize category-specific neural activity during encoding, oscillatory power was estimated for each electrode at multiple time points (20 per second) and frequency bins (37, logarithmically spaced) relative to each study event. A separate cross-validation classification analysis was carried out for each time and frequency bin, providing the classifier with topographic patterns (across 129 electrodes) of oscillatory activity to discriminate the three categories from one another. As shown in Fig. 3A, classifier performance early after stimulus onset (roughly 0–500 ms) is relatively high for a wide range of frequencies from about 2–25 Hz, with peak performance in the theta band. In the later period (500–2000 ms), classifier performance dropped somewhat, but remained above chance, with peaks in the delta and alpha bands.

We next examined individual electrodes in order to identify electrodes with robust category-specific activity for further analysis. We carried out a separate cross-validation classification analysis at each electrode, with power at two time bins (0–500 ms and 500–2000) and all frequencies included as features. Classifier performance was significantly above chance at all electrodes ($p < 0.05$, Bonferroni corrected), but performance varied substantially between different electrodes (Fig. 3B). We used average linkage clustering to separate electrodes into two clusters based on classifier performance, and selected the high-performance cluster, which included a number of posterior electrodes (Fig. 3B), for further analysis. Previous work has shown laterality differences in EEG activity related to stimulus category (Bentin et al., 1996), which motivated us to divide the posterior cluster into left and right posterior regions of interest (ROIs), excluding two electrodes on the midline. We added 2 electrodes to the left ROI to make it symmetric with the right ROI, and to equate the number of electrodes in each ROI (Fig. 3C; also see Supplementary material). Subsequent analyses focused on these two ROIs and six frequency bands of interest: delta (2–4 Hz), theta (4–8 Hz), alpha (10–14 Hz), beta (16–25 Hz), low gamma (25–55 Hz), and high gamma (65–128 Hz). Supplementary Fig. 3 shows mean classifier performance for each frequency band and ROI. Given that our ROIs were chosen on the basis of classifier performance for the individual electrodes, estimates of mean classifier performance in the ROIs may be inflated. However, because the ROIs were selected based on data aggregated over all conditions, this selection step does not bias subsequent analysis of differences between the experimental conditions.

We first examined whether classifier performance varied with serial position or distraction condition. For each frequency band and ROI, we carried out a two-way repeated-measures ANOVA with Greenhouse-Geisser correction for nonsphericity, with serial position group (early: 1–12; late: 13–24) and distraction condition as factors. We found no significant main effects or interactions (all $p > 0.05$, Bonferroni corrected). In other words, the category-specific activity patterns identified by the classifier at each frequency band and ROI were insensitive to position in the list and to the presence of substantial inter-item distraction, at least in terms of a classifier's ability to determine the category of a studied item. However, as discussed in the next section, inter-item distraction altered other properties of category-specific activity during encoding.

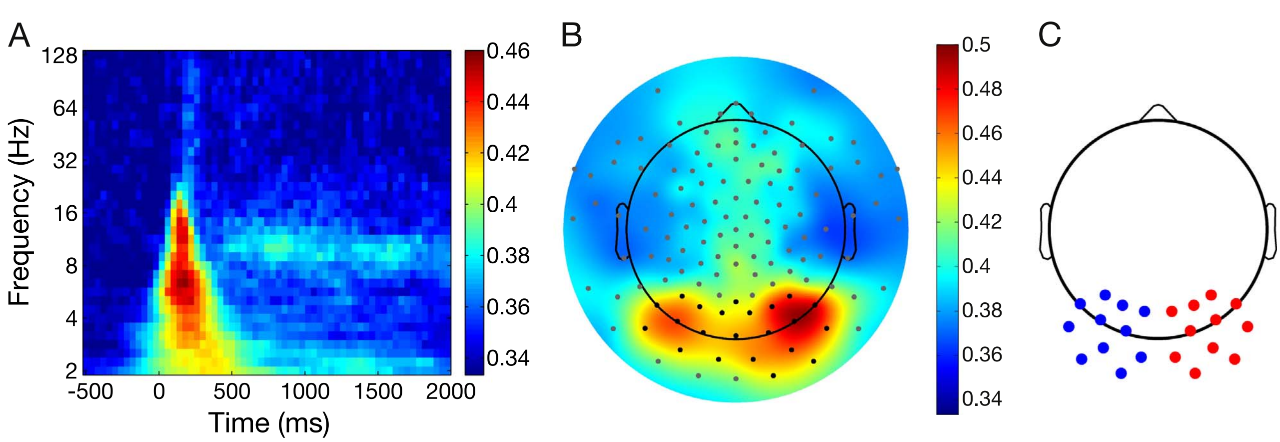

Fig. 3. (A) Classifier accuracy for separate cross-validation analyses at each time and frequency bin during item encoding. Stimuli were classified based on oscillatory power over all electrodes. Deep blue corresponds to chance performance ($0.\overline{33}$). (B) Classifier accuracy for separate cross-validation analyses at each electrode. Stimuli were classified based on oscillatory power at all frequencies and two time bins. Electrodes were divided into two clusters based on classifier performance. Electrodes in the high-accuracy cluster (shown in black) were selected for further analysis. (C) Regions of interest were determined by dividing selected electrodes into right (red) and left (blue) hemispheres; the left ROI was expanded slightly to be symmetric with the right ROI, so it would contain the same number of electrodes.

Neural evidence of integrative category-specific activity

The logistic regression classifier we used to decode stimulus category estimates the probability that a given pattern of neural activity belongs to each of three categories; we refer to these probability scores as classifier evidence. In the introduction, we describe two predictions of buffer models and retrieved-context models of episodic memory: Classifier evidence for the current category should increase as multiple items from a category are presented in succession, and the classifier should show residual (and gradually fading) evidence for the identity of the previous category (Fig. 1C). In order to test these two model predictions, we examined classifier evidence at electrodes in two ROIs that were selected based on the classifier's overall accuracy in decoding stimulus category (Fig. 3B).

For each distraction condition, ROI, and frequency band, we examined whether classifier evidence for the activation of the currently presented category changed with train position. Following the analysis methods of Morton et al. (2013), and because each train had a minimum length of 3, we calculated the slope over train positions 1–3. We take a positive slope as evidence for *neural category integration*, in that it suggests that information related to previous stimuli is being maintained in the neural system. We tested whether this slope was significantly positive for each of the two ROIs, six frequency bands, and three distraction conditions. In the IFR and CDS conditions, we observed a significantly positive slope in the right posterior ROI, in the beta band (IFR: $t(9) = 5.62$, $p = 0.012$; CDS: $t(9) = 5.23$, $p = 0.020$; Bonferroni corrected over ROIs, frequency bands, and distraction conditions). All other slopes were not significantly different from zero. The slope in the beta band in the right posterior ROI was positive for each individual participant in both the IFR and CDS conditions. Furthermore, this effect was highly specific; the slopes in all other frequency bands and ROIs were not significantly different from zero even when using a more liberal criterion of $p < 0.01$, uncorrected. Fig. 4A shows average classifier evidence for each condition and train positions 1–3, and Fig. 4D shows average slope over subjects for each condition.

Neural category integration was selective to oscillatory patterns in the beta band, in the right posterior ROI. In order to characterize this effect, we carried out a two-way repeated measures ANOVA, with stimulus category and distraction condition as factors, and slope as the dependent variable. We found no main effect of category ($F(2, 18) = 3.00$, $p = 0.075$), a main effect of distraction ($F(2, 18) = 4.32$, $p = 0.029$), and no interaction ($F < 1$). This suggests that the increase in classifier evidence with train position was not restricted to one category. We next examined each category and distraction condition separately to further characterize changes in category-specific activity with train position. Based on our predictions (Fig. 1C), we tested for positive slope over train position for each category and distraction condition, using a series of one-sided t-tests. In IFR, there was a significantly positive slope for each category (celebrities: $t(9) = 2.71$, $p = 0.012$, locations: $t(9) = 2.42$, $p = 0.02$, objects: $t(9) = 3.15$, $p = 0.006$). In the CDS condition, locations and objects had a significantly positive slope (locations: $t(9) = 1.85$, $p = 0.049$; objects: $t(9) = 2.44$, $p = 0.019$); the slope for celebrities was not greater than zero ($p > 0.05$). In the CDL condition, celebrities had a significantly positive slope ($t(9) = 1.92$, $p = 0.043$); the slopes for the other categories were not significantly positive ($p > 0.05$).

A second prediction of retrieved-context and buffer models is that activity related to a given category should persist into the next train of stimuli (as in Fig. 1C). To determine whether this effect was present in the current experiment, we used a similar procedure as above, but instead of examining the classifier evidence for activity related to the currently presented category, we examined classifier evidence for the category presented in the previous train. We calculated the slope of this evidence over train positions 1–3 to determine whether activity related to the previously presented category slowly decays as a new category is presented. We only observed a significantly negative slope in the right posterior ROI, in the beta band, during IFR ($t(9) = 4.80$, $p = 0.036$, Bonferroni corrected; Fig. 4B, D). Slope in this ROI and frequency band did not vary by category ($F < 1$) or distraction condition ($F(2, 18) = 1.34$, $p = 0.29$), and there was no interaction ($F < 1$). To further examine right posterior beta-band activity in IFR, we used a series of one-sided t-tests to test our prediction of a negative slope for the previous-category evidence, separately for each category. Celebrities ($t(9) = 2.34$, $p = 0.022$) and objects ($t(9) = 2.08$, $p = 0.034$) had significantly negative slope, while slope for locations was not different from zero ($p > 0.05$).

Because neural signals consistent with one category may also provide evidence against activation of another category, classifier evidence for the three categories may not be independent. This raises the possibility that the gradual decline in evidence for the previous category is a consequence of the rise in evidence for the current category, and is not evidence of a fading representation of the previous category. To rule out this possibility, we examined classifier evidence for a baseline category, which was neither the currently presented category or the previously presented category (Fig. 1C). For the baseline category, we found that no slopes in any ROI were significantly different from zero in any frequency band ($p > 0.05$, Bonferroni corrected; Fig. 4C–D). We predicted that the slope for the previous category should be more negative than the baseline category (Fig. 1C). A direct comparison of the slope estimates for the previous category against the baseline category (in the beta band, in the right posterior ROI, during IFR) revealed a trend towards the previous category slope being more negative than the slope of the baseline category ($t(9) = 1.47$, $p = 0.087$, one-sided test), consistent with our predictions. These results provide further evidence that oscillatory activity during episodic encoding contains information related to the recent history of presented stimuli. Furthermore, as detailed in the Supplementary material, we reexamined the data from Morton et al. (2013), and found evidence for a gradual fade of previous-category information in those data as well (Supplementary Fig. 1).

A supplementary set of analyses examined the beta-band oscillatory activity in the right posterior ROI in more detail. Supplementary Fig. 4 characterizes the category evidence slope for the current category, previous category, and baseline category in the beta band for each electrode. This analysis confirms that beta-band neural category integration effects are specific to electrodes in the right posterior ROI. Supplementary Fig. 6 shows event-locked changes in beta-band power for each category, showing an enhanced response for celebrity stimuli in the first 200 ms after stimulus presentation. This motivated us to examine whether the integrative activity in the beta band could be related to the face-selective N170 event-related potential (ERP) component (Itier and Taylor, 2004). While we did find evidence for a face-selective N170 ERP component in these data (Supplementary Fig. 6C), there was no evidence that the size of this component varied as a function of train position, suggesting that our beta-band results are distinct from the N170 ERP component (see Supplementary material for details). Furthermore, we found a similar pattern of classification results when the first 300 ms after stimulus presentation were excluded from the classification analysis, suggesting that activity sensitive to recent stimuli was not limited to early changes in beta power (Supplementary Fig. 7).

The retrieved-context model considered by Morton et al. (2013) suggests that distraction should have a progressive effect on neural category integration. In this model, persistent category information is supported by a population of integrators. During inter-item distraction, information about the distraction stimuli is integrated along with information about recently studied items (Sederberg et al., 2008), gradually pushing out category-specific activity. This raises the possibility that even in the longest distraction condition (CDL) there is some residual trace of stimulus history. To investigate this possibility, we created an integration score defined as the difference between the

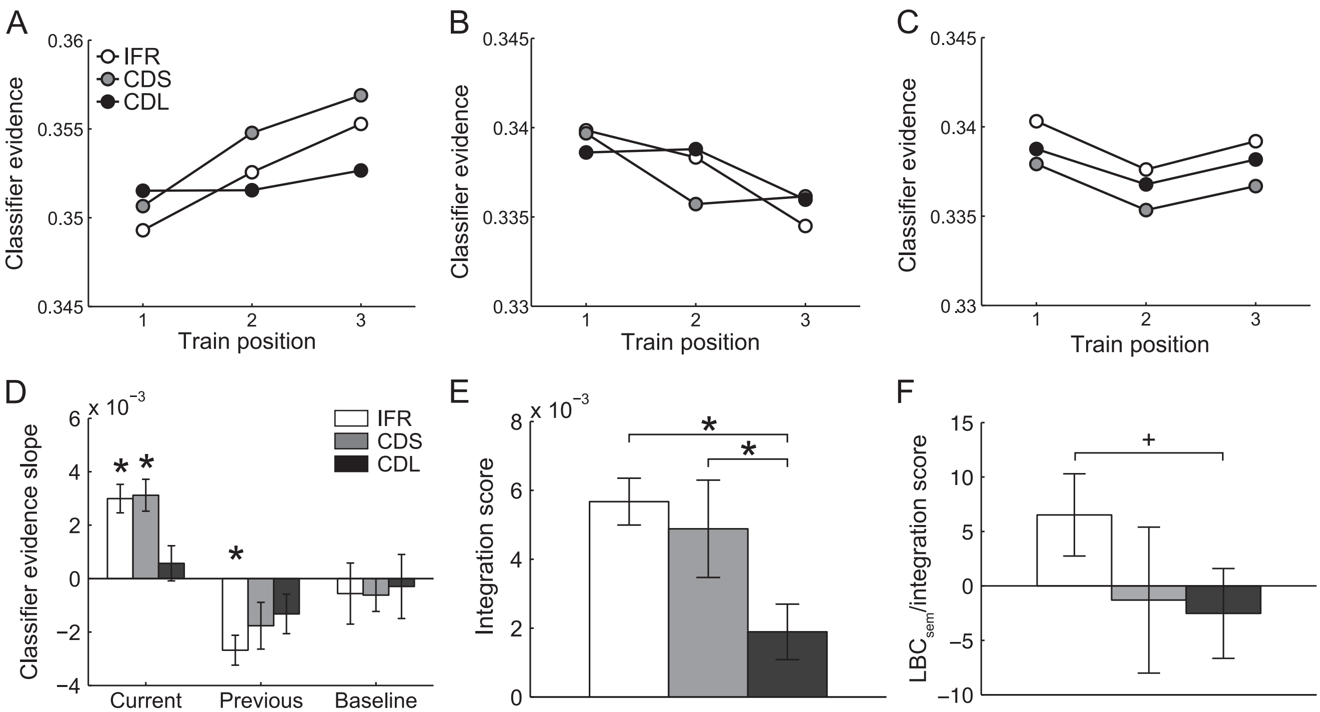

Fig. 4. Changes in classifier evidence during encoding, for beta-band activity in the right posterior region of interest. (A) Mean classifier evidence for the currently presented category, for each distraction condition and train position. (B) Mean classifier evidence for the category of the previous train. (C) Mean classifier evidence for the baseline category (neither the current or the previous category). (D) Slope of classifier evidence over train positions 1–3, for the current, previous, and baseline categories. (E) For each distraction condition, the difference between the slope of the current category and the slope of the previous category. This difference was significantly greater than zero for each distraction condition, but was decreased in the long distraction condition. (F) To obtain an estimate of how clustering varied with neural evidence for integration, we regressed LBC_{sem} for each list on integration score, separately for each participant. We found evidence for a positive relationship between integrative activity and category clustering in IFR, and this relationship was stronger in IFR compared to the CDL condition. IFR: immediate free recall; CDS: short continual distraction; CDL: long continual distraction. Error bars indicate standard error of the mean. *: $p < 0.05$. +: $p < 0.1$.

current and previous slope measures (Fig. 4E; see also Supplementary Fig. 5). The integration score was positive for IFR and CDS, and was smaller, but still significantly positive, in the CDL condition ($t(9) = 2.35$, $p = 0.043$). This suggests that relatively weak but reliable integrative activity is present even in the long distraction condition.

We predicted that inter-item distraction would have a graded effect on neural integration during encoding, with longer distraction leading to less integration; we tested this prediction with a series of one-sided t-tests. Consistent with our predictions, the neural integration score shows that inter-item distraction attenuates persistent category activity during encoding (Fig. 4E). While there was no difference between IFR and CDS ($t(9) = 0.56$, $p = 0.30$), there was a significant difference between IFR and CDL ($t(9) = 3.08$, $p = 0.0067$), and a significant difference between CDS and CDL ($t(9) = 1.85$, $p = 0.049$). These results suggest that integrative category-specific activity is attenuated by inter-item distraction.

Based on previous results (Morton et al., 2013), we predicted that decreases in integrative activity during encoding would be related to decreases in category organization during recall. Consistent with this prediction, we found that inter-item distraction resulted in both disruption of neural integration of category-specific activity (Fig. 4E) and decreased category organization (Fig. 2C). However, there was somewhat of a disconnect between these effects of distraction: While increasing distraction had a graded effect on neural category integration, we found no difference in category organization between the short- and long-distraction conditions. To better understand the potential link between integrative oscillatory activity during encoding and category organization during recall, we examined whether the amount of neural integration on a specific list correlated with the amount of category organization when that same list was recalled. Based on previous results (Morton et al., 2013), we predicted that higher integration scores would be associated with greater category clustering. To test this prediction, we first calculated LBC_{sem} and integration score for each list. For each participant, we used linear regression to estimate the relationship between integration score and category clustering across lists, separately for each distraction condition (Fig. 4F). We found a marginally significant positive slope in the IFR condition only ($t(9) = 1.82$, $p = 0.052$, one-tailed test); all other conditions $p > 0.1$. This result is consistent with the findings of Morton et al. (2013) and provides further evidence for a relationship between integrative activity during encoding and semantic organization during recall. To test whether the link between integration score and category clustering varied between conditions, we contrasted the regression slopes. There was a marginally significant difference in slope between IFR and CDL ($t(9) = 1.84$, $p = 0.0995$; all other comparisons $p > 0.1$). This result provides preliminary evidence that inter-item distraction disrupts the relationship between integrative activity during encoding and category organization during recall. We return to this point in the discussion.

Discussion

Computational models of episodic memory propose that as an experience unfolds, information about a specific stimulus persists past the time of its original occurrence, allowing the system to associate temporally disparate events with one another (Raaijmakers and Shiffrin, 1980; Davelaar et al., 2005; Howard and Kahana, 2002a; Sederberg et al., 2008; Lehman and Malmberg, 2013). Buffer-based models of working memory propose that information related to recently studied items will be maintained by neural circuitry implementing a form of short-term storage. By these models, the buffer has a fixed capacity; information related to new items can push out information related to older items. Retrieved-context models propose that a neural representation of context holds information related to recently studied items. The context representation does not have a fixed capacity; new information pushes old information out gradually. The neural results from the current study are consistent with both classes of models, which predict that information related to recent stimuli will persist for some time after the stimulus has left the environment.

We refined the data collection and analysis methods of Morton et al. (2013) in a number of ways to improve our ability to measure changes in patterns of oscillatory activity over time. We collected a larger amount of data for each participant, altered the experimental protocol to decrease perceptual differences between stimuli and minimize eye movements, and used advanced artifact-rejection methods to minimize the influence of ocular and muscle artifacts. These changes allowed us to characterize integrative oscillatory activity in greater detail. While category-specific oscillatory activity was present at a range of electrodes and frequencies during encoding (Fig. 3A, B; Supplementary Fig. 3), we only observed integrative activity in the beta frequency band (16–25 Hz) in a cluster of right posterior electrodes (Fig. 4; Supplementary Figs. 4, 5).

Consistent with our predictions, we found that inter-item distraction disrupted this integrative activity (Fig. 4; Supplementary Fig. 7). Increased inter-item distraction also disrupted semantic organization when the items were recalled, while leaving temporal organization of the memories unaffected (Fig. 2B and C). Furthermore, we found evidence that fluctuations in the amount of integrative activity during study predicted the amount of semantic organization during recall (Fig. 4F). This finding is consistent with a recent fMRI study that found that lingering thoughts about recently presented stimuli influence subsequent organization of recall (Chan et al., in revision). However, this relationship was not observed in the lists with inter-item distraction, suggesting that disruptions in integrative activity during encoding affect how subsequent recall is organized.

Category-specific oscillatory activity reflecting the recent past

We observed beta-band activity that reflected the recent history of presented stimuli, integrating information about stimuli over time (Fig. 4). The integrative activity we observed exhibited two related properties: a gradual increase in activity related to a category as items from that category were presented in succession, and a gradual decrease in activity related to the category of recently presented items.

The observation of a gradual increase in classifier evidence for the category of the current train of items is consistent with the idea that information about each stimulus is being added to some kind of integrative representation. However, it is also consistent with alternative explanations in which the recent history of stimuli influences how the current stimulus is processed by perceptual and attentional systems. For example, it could be that as a participant studies multiple items from the same category, they attend to the features of the items that are prototypical to that category, leading to a neural representation that is easier to classify (Davis and Poldrack, 2014; Iordan et al., 2016). However, this explanation would have difficulty accounting for the gradual decline in classifier evidence for the category identity of the items in the previous train, compared to the unchanging evidence of the baseline category, which had not been recently seen (Fig. 1C). This decline suggests that information related to those prior items persists in the neural system past the time of their presentation onscreen, consistent with both buffer and retrieved-context models.

While integrative activity in the beta band was attenuated by inter-item distraction, we did not observe any differences in overall classifier accuracy between the distraction conditions. While the category-specific beta-band activity we observed appears to contain information about recently presented stimuli, it may also reflect processes specific to perception of stimuli currently being presented. Non-integrative category-specific beta activity may provide a base level of classification performance, while integrative activity would either reduce classification performance (if one has just shifted to a new category) or enhance performance (if one has seen a few items from the same category in a row). These enhancements and reductions may cancel each other out, leaving average classification performance unaffected by inter-item distraction.

Oscillatory neural activity and working memory

The idea of a short-term storage buffer has greatly informed current neuroscientific models of working memory. The basic form of such a model suggests that neural activity corresponding to a study item is maintained in an active state via recurrent synaptic connections (Goldman-Rakic, 1995; Miller et al., 1996; Miller and Cohen, 2001). As long as the pattern is active, the item is considered to be held in working memory. However, a number of alternative models propose a more dynamic system in which oscillatory activity allows the system to maintain information without being in a static state (Lisman and Idiart, 1995; Axmacher et al., 2010; Lundqvist et al., 2011, 2016).

In studies using intracranial recordings or magnetoencephalography, activity in the gamma band has been linked to working memory load (Howard et al., 2003), and supports classification of stimulus identity (Jacobs and Kahana, 2009; Fuentemilla et al., 2010). In the current study, we did not observe integrative activity in the gamma band. One possible reason for this is that attenuation of high-frequency activity at the scalp may have decreased the signal-to-noise ratio in the gamma band (Nunez and Srinivasan, 2006). Although classifier performance in the gamma band is numerically above chance, it is substantially lower than beta-band performance (Fig. 3a, Supplementary Fig. 3). Morton et al. (2013) examined the category-specificity of oscillations in the low gamma (25–55 Hz) and high gamma (65–100 Hz) frequency bands, both for scalp EEG and intracranial electrocorticography (ECoG), while participants performed similar tasks. They found that with ECoG, patterns of high-gamma activity were highly category-specific; high-gamma patterns were substantially more informative for a pattern classifier compared to low-gamma patterns. In contrast, no such difference was seen with scalp EEG; low-gamma and high-gamma patterns were associated with equivalent (and relatively low) classification performance, suggesting that high-frequency category-specific activity is substantially attenuated at the scalp.

A recent study by Lundqvist et al. (2016) suggests that studied items in a working memory experiment may elicit a non-stationary pattern of neural activity, with cortical circuits alternating between high gamma and beta oscillations after stimulus presentation. They propose that this activity serves to rapidly alter synaptic connections to create a stable working memory representation that does not require uniformly sustained activity (Lundqvist et al., 2011, 2016). Given that high-gamma oscillations may be attenuated in scalp EEG, it is possible that the present study is characterizing half of this dynamic system, namely the pattern of beta oscillatory power reflecting the identities of recently studied stimuli. If items from a particular category all elicit similar spatiotemporal patterns of beta/gamma activity, the rapid alteration of synaptic connectivity could cause the global pattern of oscillations following a stimulus to reflect the identities of the last few items in the study sequence.

Implications for models of episodic memory

In the current study, inter-item distraction attenuated recall performance (Fig. 2A) relative to a condition with no distraction, consistent with prior studies (Howard and Kahana, 1999; Lohnas and Kahana, 2014). This finding is consistent with both buffer models and retrieved-context models. In buffer models, integrative activity during encoding influences the associations that are formed between studied items. In retrieved-context models integrative activity influences the associations between studied items and a representation of the context of the study episode. We found that inter-item distraction disrupted the semantic organization of memories, without affecting their temporal organization. This has also been observed previously in random word lists (Howard and Kahana, 2002b), although to our knowledge not in lists with strong category structure. This dissociation between temporal and semantic organization in their response to inter-item distraction provides a puzzle for existing models of episodic memory search to address. Here, we discuss the theoretical implications of our findings for buffer models and retrieved-context models.

Buffer models assume that studied items are placed into a limited-capacity working-memory buffer, and that items that simultaneously occupy the buffer become associated to one another (e.g. Raaijmakers and Shiffrin, 1980). Theorists have proposed that co-occupancy in the buffer facilitates the discovery of semantic associations between a pair of items (Glanzer, 1969; Anderson, 1972; Howard and Kahana, 2002b). Pure dual-store models like SAM (Raaijmakers and Shiffrin, 1980) or FRAN (Anderson, 1972) may be able to account for the decrease in semantic organization with increasing inter-item distraction by assuming that distraction empties out short-term memory, preventing semantic relationships from being discovered during encoding. This account is consistent with our observation that integrative category-specific oscillatory activity was attenuated by distraction. However, traditional buffer models have difficulty accounting for the finding that temporal organization is not affected by inter-item distraction (Davelaar et al., 2005). The context-activation model, which proposes that memory search is guided by the combined operation of a limited-capacity buffer and a representation of temporal context, can account for the insensitivity of temporal organization to distraction (Davelaar et al., 2005). Furthermore, this model assumes that semantically related items that co-occur in the buffer will tend to be active in the buffer for a longer time than items that are not semantically related, leading to stronger associations between related items. Because this effect relies on multiple items being in the buffer at the same time, it will be attenuated by inter-item distraction, which displaces items from the buffer (Davelaar et al., 2006). As such, the context-activation model may be able to account for the effect of distraction on integrative oscillatory activity, though explicit simulations are necessary to determine whether the model can account for reduced category organization in the distraction conditions while simultaneously capturing the insensitivity of temporal organization to distraction.

Retrieved-context models may also be able to account for our findings. Retrieved-context models assume that information about items is integrated into a gradually changing representation of temporal context. When an item is studied, it both alters the state of temporal context and becomes associated to the temporal context representation (Howard and Kahana, 2002a). During recall, this representation of temporal context is used as a retrieval cue, prompting the system to retrieve associated item representations. When a given item is remembered, the system also retrieves the state of temporal context associated with its original occurrence. When this retrieved context is used as part of the retrieval cue, it tends to support the retrieval of other items studied nearby in time to the last item recalled, giving rise to temporal organization (Howard and Kahana, 2002a). Inter-item distraction is proposed to partially disrupt temporal context (Sederberg et al., 2008), causing items from neighboring list positions to be associated with less similar contextual cues. However, when the context associated with a particular item is retrieved, that item's neighbors are still (relatively speaking) the best supported items in the ensuing retrieval competition, as the more distant neighbors are pushed even further away by the inter-item distraction. As a result, retrieved-context models can account for the finding that temporal organization occurs in free recall even when study items are separated by inter-item distraction (Howard and Kahana, 1999; Sederberg et al., 2008).

With regard to semantic organization, two types of retrieved-context models of this phenomenon have been proposed. Polyn et al. (2009) proposed that while each item is studied, it causes semantic information to be integrated into context; this context is later used to guide retrieval, resulting in semantic organization. Morton and Polyn (2016) contrasted this with an alternative model in which temporal and semantic cues are independent, and found that the independent cues model provided a much better account for recall behavior in free recall of random word lists. However, the current results are most consistent with the Polyn et al. (2009) model, in which semantic information can be integrated into temporal context during encoding, causing increased semantic organization during recall. A possible reason for this discrepancy is the difference in the study materials: When participants study lists of categorized stimuli, the category structure of the lists may be particularly salient, causing semantic information to influence the evolution of temporal context to a greater degree than during study of a series of random words.

While the retrieved-context model proposed by Polyn et al. (2009) appears consistent with our observation of a link between integrative category-specific activity during encoding and increased category organization, it is unclear whether this model will be able to account for the dissociation between temporal and semantic organization. One approach to adapting retrieved-context models to account for this finding would be to assume that distraction selectively affects integration of semantic information into context, while leaving other influences on context evolution relatively unaffected, thus preserving a temporal cue while disrupting semantic cuing.

More generally, our results are consistent with the hypothesis that inter-item distraction affects recall by disrupting integration of category information during encoding, leading to a decreased use of category cues during recall. However, it should be noted that the effect of distraction on category clustering and neural integration were somewhat different: Category organization was reduced in both the short and long distraction conditions (Fig. 2C), while neural integration was only significantly reduced in the long distraction condition (Fig. 4E). One possible reason for this discrepancy is that small disruptions in integrative neural activity may lead to relatively large changes in recall organization. For example, a partial activation of a recently presented item may not be sufficient to facilitate the discovery of semantic relationships between that item and the item currently being studied, resulting in a weaker association between those items in memory. This interpretation is supported by our finding that the strength of integrative oscillatory activity during encoding predicted the amount of category organization during recall, but only in the no-distraction condition (Fig. 4F).

Overall, our results provide evidence that patterns of oscillatory activity contain information about the recent history of presented stimuli, as predicted by several influential models of episodic memory. Furthermore, we find that distraction disrupts this activity, providing a potential explanation for decreased semantic organization during memory search. Our results provide a potential link between cognitive models describing the representation of one's recent history and patterns of oscillatory neural activity, and provide important constraint for theories of episodic memory.

Acknowledgments

This research was partially carried out as part of NWM's doctoral dissertation with SMP at Vanderbilt University. This work was supported by NSF Grant 1157432 and a Vanderbilt University Discovery Grant. Thanks to Micajah Spoden and Joshua McCluey for help with data collection. Thanks to Gordon Logan, Geoff Woodman, Brandon Ally, James Kragel, Michael Mack, and Richard Arriviello for helpful discussions.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuroimage.2016.12.049.

References

Anderson, J.R., 1972. FRAN: A simulation model of free recall. In: Bower, G.H. (Ed.), The Psychology of Learning and Motivation 5. Academic Press, New York, 315–379.
Axmacher, N., Henseler, M., Jensen, O., Weinreich, I., Elger, C., Fell, J., 2010. Cross-frequency coupling supports multi-item working memory in the human hippocampus. Proc. Natl. Acad. Sci. USA 107 (7), 3228–3233.
Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8 (6), 551–565.
Bousfield, W.A., 1953. The occurrence of clustering in the recall of randomly arranged associates. J. General. Psychol. 49, 229–240.
Brown, G.D.A., Neath, I., Chater, N., 2007. A temporal ratio model of memory. Psychol. Rev. 114 (3), 539–576.
Chan, S.C.Y., Applegate, M.C., Morton, N.W, Polyn, S.M., Norman, K.A., Lingering representations of stimuli influence recall organization, In revision
Davelaar, E.J., Goshen-Gottstein, Y., Ashkenazi, A., Haarmann, H.J., Usher, M., 2005. The demise of short-term memory revisited: Empirical and computational investigations of recency effects. Psychol. Rev. 112, 3–42.
Davelaar, E.J., Haarmann, H.J., Goshen-Gottstein, Y., Usher, M., 2006. Semantic similarity dissociates short-term from long-term recency effects: Testing a neurocomputational model of list memory. Mem. Cogn. 34 (2), 323–334.
Davis, T., Poldrack, R.A., 2014. Quantifying the internal structure of categories using a neural typicality measure. Cereb. Cortex 24 (7), 1720–1737.
Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics. J. Neurosci. Methods 134, 9–21.
DuBrow, S., Davachi, L., 2014. Temporal memory is shaped by encoding stability and intervening item reactivation. J. Neurosci. 34 (42), 13998–14005.
Duda, R.O., Hart, P.E., Stork, D.G., 2001. Pattern Classification second edition. Wiley, New York.
Estes, W.K., 1955. Statistical theory of spontaneous recovery and regression. Psychol. Rev. 62, 145–154.
Fuentemilla, L., Penny, W.D., Cashdollar, N., Bunzeck, N., Düzel, E., 2010. Theta-coupled periodic replay in working memory. Curr. Biol. 20 (7), 606–612.
Glanzer, M., 1969. Distance between related words in free recall: Trace of the STS. J. Verbal Learn. Verbal Behav. 8, 105–111.
Glenberg, A.M., Bradley, M.M., Stevenson, J.A., Kraus, T.A., Tkachuk, M.J., Gretz, A.L., 1980. A two-process account of long-term serial position effects. J. Exp. Psychol.: Hum. Learn. Mem. 6, 355–369.
Goldman-Rakic, P., 1995. Cellular basis of working memory. Neuron 14, 477–485.
Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science 293, 2425–2429.
Howard, M.W., Kahana, M.J., 1999. Contextual variability and serial position effects in free recall. J. Exp. Psychol.: Learn. Mem. Cogn. 25, 923–941.
Howard, M.W., Kahana, M.J., 2002a. A distributed representation of temporal context. J. Math. Psychol. 46, 269–299.
Howard, M.W., Kahana, M.J., 2002b. When does semantic similarity help episodic retrieval? J. Mem. Lang. 46, 85–98.
Howard, M.W., Rizzuto, D.S., Caplan, J.C., Madsen, J.R., Lisman, J., Aschenbrenner-Scheibe, R., Schultze-Bonhage, A., Kahana, M.J., 2003. Gamma oscillations correlate with working memory load in humans. Cereb. Cortex 13, 1369–1374.
Hsieh, L.-T., Gruber, M.J., Jenkins, L.J., Ranganath, C., 2014. Hippocampal activity patterns carry information about objects in temporal context. Neuron 81 (5), 1165–1178.
Iordan, M.C., Greene, M.R., Beck, D.M., Fei-Fei, L., 2016. Typicality sharpens category representations in object-selective cortex. NeuroImage 134, 170–179.
Itier, R., Taylor, M., 2004. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. Cereb. Cortex 14 (2), 132–142.
Jacobs, J., Kahana, M.J., 2009. Neural representations of individual stimuli in humans revealed by gamma-band ECoG activity. J. Neurosci. 29 (33), 10203–10214.
Jenkins, L.J., Ranganath, C., 2010. Prefrontal and medial temporal lobe activity at encoding predicts temporal context memory. J. Neurosci. 30 (46), 15558–15565.
Jung, T.-P., Makeig, S., Westerfield, M., Townsend, J., Courchesne, E., Sejnowski, T.J., 2001. Analysis and visualization of single-trial event-related potentials. Hum. Brain Mapp. 14 (3), 166–185.
Junghöfer, M., Elbert, T., Tucker, D.M., Rockstroh, B., 2000. Statistical control of artifacts in dense array EEG/MEG studies. Psychophysiology 37 (4), 523–532.
Kahana, M.J., 1996. Associative retrieval processes in free recall. Mem. Cogn. 24, 103–109.
Kahana, M.J., 2012. Foundations of Human Memory 1st Edition. University Press, New York, NY.
Kimball, D.R., Smith, T.A., Kahana, M.J., 2007. The fSAM model of false recall. Psychol. Rev. 114 (4), 954–993.
Kriegeskorte, N., Mur, M., Ruff, D.A., Kiani, R., Bodurka, J., Esteky, H., Tanaka, K., Bandettini, P.A., 2008. Matching categorical object representations in inferior temporal cortex of man and monkey. Neuron 60, 1126–1141.
Kuhl, B.A., Rissman, J., Wagner, A.D., 2012. Multi-voxel patterns of visual category representation during episodic encoding are predictive of subsequent memory. Neuropsychologia 50, 458–469.
LaRocque, K.F., Smith, M.E., Carr, V.A., Witthoft, N., Grill-Spector, K., Wagner, A.D., 2013. Global similarity and pattern separation in the human medial temporal lobe predict subsequent memory. J. Neurosci. 33 (13), 5466–5474.
Lehman, M., Malmberg, K.J., 2013. A buffer model of memory encoding and temporal correlations in retrieval. Psychol. Rev. 120 (1), 155–189.
Lisman, J., Idiart, M.A., 1995. Storage of 7 ± 2 short-term memories in oscillatory subcycles. Science 267, 1512–1515.
Lohnas, L.J., Kahana, M.J., 2014. Compound cuing in free recall. J. Exp. Psychol.: Learn. Mem. Cogn. 40 (1), 12–24.
Lohnas, L.J., Polyn, S.M., Kahana, M.J., 2015. Expanding the scope of memory search: Modeling intralist and interlist effects in free recall. Psychol. Rev. 122 (2), 337–363.
Lundqvist, M., Herman, P., Lansner, A., 2011. Theta and gamma power increases and alpha/beta power decreases with memory load in an attractor network model. J. Cogn. Neurosci. 23 (10), 3008–3020.
Lundqvist, M., Rose, J., Herman, P., Brincat, S.L., Buschman, T.J., Miller, E.K., 2016. Gamma and beta bursts underlie working memory. Neuron 90 (1), 152–164.
Manning, J.R., Polyn, S.M., Baltuch, G., Litt, B., Kahana, M.J., 2011. Oscillatory patterns in temporal lobe reveal context reinstatement during memory search. Proc. Natl. Acad. Sci. USA 108 (31), 12893–12897.
McMenamin, B.W., Shackman, A.J., Maxwell, J.S., Bachhuber, D.R.W., Koppenhaver, A.M., Greischar, L.L., Davidson, R.J., 2010. Validation of ICA-based myogenic artifact correction for scalp and source-localized EEG. NeuroImage 49 (3), 2416–2432.
Mensink, G.-J.M., Raaijmakers, J.G.W., 1989. A model for contextual fluctuation. J. Math. Psychol. 33, 172–186.
Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24, 167–202.
Miller, E.K., Erickson, C.A., Desimone, R., 1996. Neural mechanisms of visual working memory in prefrontal cortex of the macaque. J. Neurosci. 16, 5154.
Morton, N.W., Kahana, M.J., Rosenberg, E.A., Baltuch, G.H., Litt, B., Sharan, A.D., Sperling, M.R., Polyn, S.M., 2013. Category-specific neural oscillations predict recall organization during memory search. Cereb. Cortex 23 (10), 2407–2422.
Morton, N.W., Polyn, S.M., 2016. A predictive framework for evaluating models of semantic organization in free recall. J. Mem. Lang. 86, 119–140.
Newman, E.L., Norman, K.A., 2010. Moderate excitation leads to weakening of perceptual representations. Cereb. Cortex 20 (11), 2760–2770.
Nolan, H., Whelan, R., Reilly, R.B., 2010. FASTER: Fully automated statistical thresholding for EEG artifact rejection. J. Neurosci. Methods 192 (1), 152–162.
Norman, K.A., Polyn, S.M., Detre, G.J., Haxby, J.V., 2006. Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. Trends Cogn. Sci. 10 (9), 424–430.
Nunez, P., Srinivasan, R., 2006. Electric Fields of the Brain: The Neurophysics of EEG. Oxford University Press, New York.
Onton, J., Westerfield, M., Townsend, J., Makeig, S., 2006. Imaging human EEG dynamics using independent component analysis. Neurosci. Biobehav. Rev. 30 (6), 808–822.
Polyn, S.M., Erlikhman, G., Kahana, M.J., 2011. Semantic cuing and the scale-insensitivity of recency and contiguity. J. Exp. Psychol.: Learn. Mem. Cogn. 27 (3), 766–775.
Polyn, S.M., Natu, V.S., Cohen, J.D., Norman, K.A., 2005. Category-specific cortical activity precedes retrieval during memory search. Science 310, 1963–1966.
Polyn, S.M., Norman, K.A., Kahana, M.J., 2009. A context maintenance and retrieval model of organizational processes in free recall. Psychol. Rev. 116 (1), 129–156.
Puff, C.R., 1979. Memory organization research and theory: The state of the art. In: Puff, C.R. (Ed.), Memory Organization and Structure. Academic Press, New York, 3–17, (Ch. 1).
Raaijmakers, J.G.W., Shiffrin, R.M., 1980. SAM: A theory of probabilistic search of associative memory. In: Bower, G.H. (Ed.), The Psychology of Learning and Motivation: Advances in Research and Theory 14. Academic Press, New York, 207–262.
Raaijmakers, J.G.W., Shiffrin, R.M., 1981. Search of associative memory. Psychol. Rev. 88, 93–134.
Rogers, T.T., McClelland, J.L., 2004. Semantic Cognition: A Parallel Distributed Processing Approach. MIT Press, Cambridge, MA.
Schacter, D.L., 1987. Memory, amnesia, and frontal lobe dysfunction. Psychobiology 15, 21–36.
Sederberg, P.B., Howard, M.W., Kahana, M.J., 2008. A context-based theory of recency and contiguity in free recall. Psychol. Rev. 115 (4), 893–912.
Sirotin, Y.B., Kimball, D.R., Kahana, M.J., 2005. Going beyond a single list: Modeling the effects of prior experience on episodic free recall. Psychon. Bull. Rev. 12 (5), 787–805.
Stricker, J.L., Brown, G.G., Wixted, J.T., Baldo, J.V., Delis, D.C., 2002. New semantic and serial clustering indices for the California Verbal Learning Test—Second Edition: Background, rationale, and formulae. J. Int. Neuropsychol. Soc. 8, 425–435.
Tulving, E., 1983. Elements of Episodic Memory. Oxford, New York.
Willenbockel, V., Sadr, J., Fiset, D., Horne, G.O., Gosselin, F., Tanaka, J.W., 2010. Controlling low-level image properties: The SHINE toolbox. Behav. Res. Methods 42 (3), 671–684.
Zacks, J., Tversky, B., 2001. Event structure in perception and conception. Psychol. Bull. 127 (1), 3.